SUMMARIES IN MICRO-BIOLOGY

For some months the Secretary has been seeking to secure for this Journal and its Department of Summaries, a series of papers from biologists dealing with the chief groups of microscopic plants and animals. It has not been the purpose to present a complete survey of any of the groups. The wish has been rather to bring together in one article a statement of the following things:—general biology, the method of finding, the methods of capture and of keeping alive and cultivating in the laboratory; how best to study; the general technic; the most accessible literature; and a brief outline of the classification, with keys for the identification of at least the more representative genera and species of the micro-organisms likely to be found by the beginning students in the United States.

It has been felt that the getting together of such data as this, while not a contribution to science, would be a contribution especially to isolated workers and to teachers and students in the high schools and smaller colleges.

Papers have already appeared treating the aquatic Oligochetes, the Melanconiales, the Rusts, and Black Moulds. The following is the fifth paper of the series. It is proposed to have such synopses from time to time until the more common American species of such groups as the following have been covered: The Blue-green Algae, Conjugating Algae, Diatoms, other Green Algae, Downy Mildews, Yeasts, Hyphomycetes, Smuts, Rhizopods, Infusoria, Turbellaria, Bryozoa, Water Mites, Entomostraca, etc.—[Editor.]

THE POWDERY MILDEWS—ERYSIPHACEÆ

By George M. Reed

Introduction. The Erysiphaceæ constitute a well defined group of the Ascomycetes. Various common names are applied to these fungi, as mildew, powdery mildew, white mildew, blight. They have long been interesting forms for study, partly on account of the microscopical interest in observing the fruiting bodies with their characteristic and frequently ornate appendages, but more especially on account of their parasitic nature, in many cases being of considerable economic importance due to the injury caused to various seed plants.

The powdery mildews are obligate parasites, attacking various Angiosperms. In fact these parasites are mainly limited to the Dicotyledons, only one species being reported as common upon Monocotyledons—*Erysiphe graminis* on members of the grass family.

The group is characterized by the possession of two distinct fruiting stages. One, the conidial stage, develops during the summer and results in the formation of a very large number of white,

more or less ellipsoidal spores which are easily distributed by air currents. This stage has been referred to a distinct genus, *Oidium*, belonging to the Fungi Imperfecti. It is now described as the Oidial, or better still, the conidial stage. Later in the season the ascus stage of the fungus is produced. The asci, one or more, are borne within the fruiting bodies or ascocarps. The latter are small, more or less globular, dark brown or black structures without differentiated openings for the escape of the asci or ascospores. These ascocarps, or perithecia, are provided with peculiar appendages which are outgrowths of the outer layer of cells of the perithecial wall. They are sometimes ornately branched and their characteristics are of considerable value in classification. The asci are sac-like structures, more or less oval in shape, and at maturity contain two to eight ascospores depending upon the species. In general the conidial stage serves to spread the fungus rapidly and widely during the growing period of the host while the ascocarp stage serves to tide the fungus over the winter season.

Mycelium and Conidial Stage. With few exceptions the mycelium of the powdery mildews is external to the host tissues. It generally develops on either the upper or lower surfaces of the leaves, but frequently is found on the stems, flowers and fruits. The mycelium is generally hyaline, well developed and much branched and the hyphae which compose it are septate. Thus it is composed of many cells, each cell containing regularly one nucleus.

At numerous places on the mycelium a special hypha grows towards the host tissue, penetrates a cell of the host, and forms a haustorium. In many cases, these haustoria arise from a flattened expansion, called an appressorium, of the superficial mycelium. The haustoria function as absorbing organs and obtain the necessary materials for the mycelium from the host protoplast.

Generally these haustoria are confined to the epidermal cells. In a few cases they are formed in the deeper lying cells. For example, in *Uncinula salicis,* according to Smith (62), some hyphæ from the surface mycelium grow through the epidermal cells and form the haustorial expansions in the cells of the mesophyll tissue. (Pl. XIII, Fig. 2). Even in this mildew, however, most of the haustoria develop in the epidermal cells. In many cases, notably the

grass mildew, several of these absorbing organs may be found in a single host cell.

Smith (62) has quite fully described the haustoria of the Erysiphaceæ and their relation to the host cells. In most cases they are more or less globular swellings at the ends of the special penetrating branches (Pl. XIII, Figs. 1, 2). In the grass mildew, *Erysiphe graminis,* the haustoria seem to be highly specialized structures (Pl. XIII, Fig. 3). They consist of an ellipsoidal central portion with long finger-like processes at one or both ends. They would appear to be efficient absorbing organs and may be correlated with the vigorous development of mycelium and abundant production of conidia characteristic of this mildew. The haustoria of *E. galeopsidis* are also somewhat lobed. In fact the lobing of the haustoria of this species is the principal basis for separating it from *E. cichoracearum.*

The haustoria of all the mildews regularly contain a single nucleus; very rarely are two nuclei found in one haustorium.

As already indicated the mycelium of some mildews, in part at least, is endophytic. The mycelium of the genus Phyllactinia grows in the intercellular spaces of the mesophyll of the host leaves. The haustoria develop as side branches from the intercellular mycelium and penetrate the various host cells in the interior of the leaf.

Salmon (59) has described *Erysiphe taurica* as being even more endophytic in its habit than Phyllactinia. The mycelium is at first wholly endophytic; from this arise conidiophores which pass through the stomata to the exterior. The perithecia are developed on a superficial mycelium which originates from that in the interior of the leaf. Globular haustoria are found in the mesophyll cells of the host. Salmon has recently separated this species, on the basis of these characters, and placed it in a distinct genus—Oidiopsis.

As the mycelium develops special branches arise which grow away from the surface of the leaf. These hyphae form the conidiophores (Pl. XIII, Fig. 4), one of the fruiting stages of the fungus. At the end of each conidiophore a more or less ellipsoidal conidium is cut off. The hypha elongates again and a second conidium is cut off. This process of basipetal abstriction continues, finally resulting in the formation of a chain-like row of oval conidia, the oldest being at the apical end. These easily separate as they mature

and are readily distributed by air currents. The young cell which forms the conidiophore contains a single nucleus. Nuclear division precedes the cell division and thus each conidium comes to have a single nucleus.

The conidia germinate readily in water or moist air by pushing out one or more germ tubes. (Pl. XIII, Fig. 5). Unless applied to the proper host, however, but little growth occurs. If the conidia are placed on the proper host, mycelia with their haustoria are quickly developed which soon give rise to other crops of conidia. In the grass mildew 48-72 hours are sufficient for this cycle of development. Consequently during a single season a succession of crops of conidia may be formed and many millions of spores may be produced.

Development of the Perithecium. Although many students of the mildews had examined carefully the structure of the mature perithecium and had worked out systems of classification based upon its characteristics, De Bary (5) in 1863, was the first to adequately trace the origin of this structure. He studied the development of the perithecium of *Sphaerotheca castagnei* on Taraxacum. De Bary (6) later (1871) studied other forms and found their development essentially similar to that of *Sphaerotheca.*

De Bary describes the ascocarp or perithecium as arising at the point of contact or crossing of two branches of the mycelium. These branches push out protuberances at the same time which rise erect from the epidermis of the host. They are soon cut off by cross walls and the one from the lower hypha grows and takes the form of an elongated ellipsoidal cell. This is the archicarp or oogonium. The other branch, the antheridial branch, remains cylindrical and is closely applied to the oogonium, its upper end bending over and covering the apex of the latter. A cross wall cuts off a short nearly isodiametric cell, the antheridium, which is borne on the basal cell or stalk. The oogonium now develops into the sporocarp, usually being divided into two cells, the upper one forming the solitary ascus of this mildew while the other remains as a stalk cell to the ascus. The ascus subsequently produces eight ascospores. As the young ascus develops the envelope apparatus is formed by the outgrowth of seven to nine tubular hyphæ from the base of the oogonium and antheridium. These hyphae elongate, remaining in close contact

with each other and also with the oogonium and antheridium, finally meeting above the apex of the antheridium. Each hypha then divides by one or two transverse walls and the young sporocarp is surrounded by a single layer of cells. From the inner surfaces of these hyphae secondary branches arise which ramify and develop into a dense parenchyma-like weft formed of two or more layers of cells. From the outer layer of cells, those first formed, the appendages arise. The walls of these outer cells also thicken and assume a dark brown color.

In *Erysiphe* the main difference lies in the fact that the archicarp or oogonium grows into a curved tube and divides by transverse walls into a row of several cells. From these cells a number of club-shaped, erect asci are formed by each cell growing out into an ascus or putting out a few short branches which finally terminate in asci.

Although De Bary maintained that the perithecium originated as the result of a fusion of sex cells he was unable to determine the actual fusion of the protoplasts of the oogonium and antheridium. Harper (28, 29, 30), using modern cytological methods, has been able to verify De Bary's conclusion and has added many additional facts to the history of the development of the perithecium and the following account is based on his studies of Sphaerotheca, Erysiphe and Phyllactinia.

Both antheridium and oogonium arise as side branches of neighboring hyphae. The development of the oogonium generally preceeds that of the antheridium and it soon forms a short oval branch which can easily be distinguished from vegetative branches by being vertical to the leaf surface and also by containing denser protoplasm. After the oogonial branch has elongated until it is two to three times as high as wide, with a transverse diameter twice that of a vegetative hypha, it is separated from the latter by a cross wall. (Pl. XIV, Fig. 9). The oogonium contains a single nucleus which is hardly distinguishable from that of a vegetative cell. During this process the young antheridial branch bends up and grows close to the side of the young oogonium. After a time a cross wall is formed cutting off a single nucleated cell. After the complete formation of the oogonium the antheridial branch elongates and its nucleus divides (Pl. XIV, Fig. 10), followed by cell division which cuts off a

small terminal antheridium and a stalk cell (Pl. XIV, Figs. 11, 12). The antheridium is carried upward by growth, becomes closely appressed to the oogonium, and appears as a cap on the latter. Next the cell wall between the oogonium and antheridium is dissolved and the antheridial nucleus migrates through the opening and approaches the egg necleus which lies near the center of the oogonium (Pl. XIV, Fig. 13). The nuclei now fuse and soon the opening between the antheridium and oogonium is closed (Pl. XIV, Fig. 14).

At the same time with the entrance of the male nucleus into the oogonium the development of the perithecial wall begins (Pl. XIV, Figs. 15-20). Hyphæ arise at the base of the oogonium and grow up around the antheridium and oogonium. These become multi-cellular by nuclear and cell division. The antheridium relaxes and collapses but persists among the wall cells for some time. Next, due to the enlargement of the stalk of the oogonium, the first series of wall cells are bent out and other hyphae grow up inside them and, by branching and dividing, form a sphere of cells about the oogonium. The wall of the perithecium then contains several layers of cells, the outer for protection, the inner for nourishment. From the former the appendages arise when the perithecium is about half grown (Pl. XIII, Fig. 8). These soon become thick walled and lose their protoplasmic contents on the further ripening of the perithecium.

The fusion of the two nuclei in the oogonium takes place before the completion of the first wall layer. As further development proceeds, the oogonium grows into the ascogonium. The fusion nucleus in the oogonium first divides, following by cell division (Pl. XIV, Fig. 17); the lower cell of these two develops no further. The nucleus of the upper cell again divides and this is followed by cell division; this process is repeated until a series of five to six cells is formed (Pl. XIV, Fig. 19). Each of these cells has regularly one nucleus except the next to the last which invariably has two. This penultimate cell develops into the ascus (Pl. XIV, Fig. 20).

In the early stages the development of the mildews with several asci is similar to that of Sphaerotheca. Harper (29, 30) has carefully traced the development of sex organs and established the nuclear fusion in the young oogonium of both Erysiphe and Phyllactinia.

The oogonium, after the fusion of the antheridial and oogonial nuclei, develops into the ascogonium (Pl. XIII, Fig. 6). This is accomplished by the elongation of the oogonium which becomes curved in a very irregular fashion. Nuclear division occurs but this is not followed at once by cell division. Instead further nuclear divisons occur. Soon, however, cell division takes place and there is formed a row of three to five cells. The end cell of the fully developed ascogonium regularly contains one nucleus while the next to the last or penultimate cell always contains more than one nucleus.

Following the formation of the ascogonium, the ascogenous hyphae arise as lateral branches of the former (Pl. XIII, Figs. 6, 7). Most, if not all, of these hyphae arise from the penultimate cell. The number of cells in each hypha varies but one cell in each becomes an ascus. These cells always contain two nuclei while the other cells of ascogonium and ascogenous hyphae are almost without exception uninucleated.

During these processes the perithecial wall is formed by the upgrowth of hyphae from the stalks of both antheridium and oogonium. These, by continued division and branching, form finally the many celled wall of the perithecium (Pl. XIII, Fig. 8). When the perithecial wall is fully differentiated the further development of the asci begins.

As already noted each young ascus always contains two nuclei (Pl. XIV, Figs. 19, 21). Harper (30) has traced with exceptional completeness the nuclear phenomena which occur in the further development of the asci (Pl. XIV, Figs. 21-24, Pl. XV, Figs. 25-33). The asci rapidly increase in size and consist of an upper enlarged portion, in which the nuclei lie, and a lower stalk-like portion.

When the ascus has attained about half of its mature size the two nuclei fuse to form the primary ascus nucleus. (Pl. XIV, Figs. 22-24). The union of the two resting nuclei results in the formation of a single spherical nucleus which increases in size with the further growth of the ascus (Pl. XV, Fig. 25). This primary ascus nucleus next undergoes division resulting in the formation of two nuclei; each of these divide giving rise to four which in turn divide forming eight nuclei in the ascus (Pl. XV, Figs. 26-30). This triple division of the primary ascus nucleus is characteristic not only of the

mildews but of by far the larger number of other Ascomycetes as well.

During all the nuclear processes from the first development of the young oogonium Harper has been able to demonstrate the occurrence of a central body and to follow its behavior. This central body is located on the nuclear membrane. "It constitutes throughout a point of attachment for the elements of the nucleus, and in all the various modifications which it and they undergo in the processes of division and fusion this relation is maintained in the most definite fashion. The central body by its position determines in an important sense a definite polar organization on the part of the chromatin, and thus of the nucleus as a whole." "In every stage the chromatin is definitely attached to either one or two central bodies on the periphery of the nucleus. The nucleus is hence strictly unipolar throughout its so-called resting stages, becoming bipolar by division of the center for the formation of the two daughter nuclei." Harper has given a continuous account "of the existence of the central body and the maintainance of its connection with the material of the chromosomes through two nuclear fusions in the oogonium and in the young ascus, through a series of divisions in the ascogenous hyphae, and the triple division in the ascus, and finally through the formation of the ascospores by free cell formation." "The central bodies are thus seen to be permanent structures of the cell during both the dividing and resting stages of nuclear development."

During the process of all three nuclear divisions there is a well developed system of astral rays which extend from the central body into the cytoplasm. This polar aster persists after the third division and functions in the process of spore formation.

In Phyllactinia regularly only two ascospores are formed, each with a single nucleus. The other six nuclei formed in the triple division of the primary ascus nucleus are regarded as supernumerary nuclei which soon disintegrate in the cytoplasm. In some mildews, however, as in Sphaerotheca, all eight nuclei function and the mature ascus contains eight ascospores. In the different mildews the number of ascospores varies from two to eight.

Harper has described ascospore formation as a process of "free cell formation." Following the completion of the third nuclear division, a beak is developed on the functional nuclei which are usually more or less pear-shaped.

The central body is located at the apex of the beak. In general the beaked nucleus and aster lie free in the cytoplasm but sometimes lie quite close to the ascus wall. The astral rays are folded over to form the plasma membrane of the spore. (Pl. XV, Figs. 31, 32). "The rays become elongated during the process by growth which apparently proceeds from the central body outward, and at the same time they fold over and combine side by side to form a continuous broad, umbrella-shaped membrane. Sometimes the rays on one side seem to be in advance of those on the other in the process of enclosing the spore mass. If, in folding over and elongating, the rays of one center come in contact with those of another, they tend to fuse, at least temporarily. Later, however, they must separate again, since one almost never finds spores with two nuclei." "The broad umbrella-shaped membrane gradually closes in to form, by further marginal growth, the ellipsoidal plasma membrane of the spore. The whole spore body is cut out of the previously undifferentiated cytoplasm of the ascus by the formation of a new plasma membrane derived from the fibers of the polar aster and without the deposition of a cellulose wall."

Following the enclosure of the spore plasm by the new plasma membrane, the central body breaks away from the membrane, the nucleus regains its spherical or oval shape, with the central body lying on the surface of the nuclear membrane. Finally a wall is formed about the spores and the development of the perithecium with its ascospores is complete (Pl. XV, Fig. 33) and there follows the resting condition.

In the formation of the ascospores only a part of the cytoplasm is used up. The delimitation of the spores leaves a considerable portion of unused material. The spores thus are imbedded in the remaining part of the ascus cytoplasm. This material is called epiplasm or periplasm and its presence is a constant feature in the ascus of the Ascomycetes.

In at least two species of Erysiphe—*E. graminis* and *E. galeopsidis*—spore formation does not take place on the living host. When mature perithecia of these forms are found an examination will show the absence of the ascospores. Instead these are formed the following spring. To just what stage the nuclear phenomena proceed in the fall in these forms has not been worked out.

The ascospores escape from the perithecium in the spring. Galloway (25) states that the perithecium may suddenly burst and forcibly eject the asci. The cells of the inner wall of the perithecium, which retain their protoplasmic contents, may produce a substance capable of swelling in water and so cause the rupture of the perithecium as suggested by Harper.

The ascospores, when placed in a damp atmosphere or in water, germinate by the formation of germ tubes. If the ascospores are sown on the epidermis of a suitable host the germ tube penetrates and forms a haustorium in the host cell. The superficial mycelium also develops from this tube and, by growth and branching, soon spreads over a considerable area of host surface, giving use to numerous conidiophores.

On some hosts of the mildews perithecia are rarely formed. One noted illustration of this is the mildew on the cultivated grape in Europe. Berkeley (7) in 1847 described the conidial stage of this fungus as *Oidium Tuckeri* and, although this mildew was recognized as a serious disease, the perithecia were not observed until 1893 when Couderc (15) found these fruiting bodies and determined finally the identity of this mildew with the American *Uncinula necator*. The perithecia are quite common on grapes in this country.

In 1907, 1908 and 1909 a serious disease of various oaks in Europe, caused by a mildew, was observed by a large number of workers. The conidial stage was very common and quite destructive to the foliage of young oaks. While perithecia have since been found, they are of rare occurrence on these hosts in Europe.

It is well known that the conidial stage of *Erysiphe graminis* is very common on blue grass and other grasses but perithecia are quite infrequent. In the vicinity of Columbia *Evonymus atropurpureus* is severely attacked by a mildew but, while a large number of plants have been carefully examined by the writer, the perithecia

have not been found. Various species of Xanthium are also attacked by the conidial stage but perithecia are rarely produced.

As already noted characteristic appendages are found on the mature perithecia of the powdery mildews. These are outgrowths of the outer layer of cells of the perithecial wall. They develop from different parts of the wall in different species and show characteristic differences in their form. Their function is uncertain. In many cases, perhaps all, they serve to set the perithecium free from the surface of the leaf. In Phyllactinia for example, Neger (40) has observed the bending down of the appendages and their straightening up as a result of the alternately moistening and drying of the perithecia. In fact, in the case of the Phyllactinia, it is quite usual to find the perithecium in the mature condition turned over on the surface of the leaf so that they rarely are found in the normal position.

In addition to the characteristic appendages which are found in all the powdery mildews, certain penicillate cells develop upon the apical portions of the perithecium of Phyllactinia. These arise as an outgrowth of the cells of the outer wall of the perithecium, then grow up more or less vertically, branching repeatedly. After they have attained their full size the walls begin to swell and become gelatinous. They fuse together laterally and form a slimy mass crowning the perithecium. They serve to attach the perithecia in an inverted position to various objects, more commonly to the living epidermis of the host after the perithecia have been loosened from their place of development by the hygroscopic movements of the appendages. The perithecia may fall upon *Fomes,* as has been recorded, and be re-attached by these penicillate cells. Perhaps the unusual host distribution of this species may be, in part at least, explained by the accidental re-attachment of the perithecia.

There are several questions of great importance raised in connection with the facts of cytological study of the mildews. One question is that of the significance of the double nuclear fusion which occurs in the life history of these plants. One nuclear fusion occurs in the oogonium, when the nucleus from the antheridium migrates through the opening in the cell wall and fuses with the

egg nucleus. The second fusion occurs in the young ascus, this nuclear fusion resulting in the formation of the primary ascus nucleus.

Some investigators of this group deny that there is any fusion of nuclei in the oogonium and that the nuclear fusion which occurs in the ascus is the real fertilization process in these forms. The ascus, by these workers, is interpreted as an egg. Harper, however, has given very convincing evidence of the sexual nature of the hyphæ first described by De Bary as oogonium and antheridium and leaves no doubt as to the nuclear fusion in the oogonium. His work has also been confirmed by Blackman and Fraser (8) although denied by Dangeard (16) and more recently by Winge (72). If the nuclear fusion in the oogonium is a sexual process, as seems certain, then the subsequent nuclear fusion in the ascus cannot be considered a sexual process and the ascus cannot be interpreted as an egg.

Harper (30) has attempted to explain this second fusion on the basis of the nucleo-cytoplasmic relation. He believes that this fusion is "correlated in some way with the vegetative development of the relatively gigantic size of the ascus as compared with other cells of the fungus." Large cells in general have large or numerous nuclei and small cells have small or few nuclei. Nuclear and cytoplasmic masses are in equilibrium when there is a certain proportion between them. "Any increase in the mass of either tends toward producing a corresponding increase in the other; a reduction in one necessitates a reduction in the other, in order that the nucleo-cytoplasmic equilibrium may be maintained."

"The ascus is to be developed as a relatively large cell to serve as a storehouse, with an abundant supply of material for the formation of ascospores; and in order that the nucleo-cytoplasmic equilibrium may be maintained, it must be provided with an excess of nuclear material as compared with the other cells of the ascogenous hyphae and the ascogonium. There are several stages in this differentiation of the ascus as to its nuclear content. It is binucleated from the first, while the other cells mentioned are uninucleated; and, further, its two nuclei fuse with the union of all their corresponding parts to form a single larger nucleus, which in turn grows with the further growth of the ascus."

"In the process of spore formation we have again a most striking example of the controlling influence of the so-called nucleo-cytoplasmic relation. The nucleus of the ascus divides to form two daughter nuclei, and these in turn divide successively to form eight nuclei; but in thus passing from the uninucleated to the multinucleated condition the nucleo-cytoplasmic equilibrium is maintained. The two daughter nuclei are proportionally smaller than the mother nucleus, and the four and eight nuclei in the end bear approximately the same relation to their cytoplasmic masses as did the primary nucleus of the ascus to the cytoplasm of the entire ascus. The two nuclei which become the centers for the formation of spores grow to a somewhat larger size than the remaining six, and accordingly the mass of cytoplasm included in the two spores is more than one-fourth of that of the entire ascus."

Another fact to be explained is the universal triple division which occurs in the ascus of the powdery mildews as well as in that of all the higher Ascomycetes. The fusion nucleus regularly divides three times in rapid succession forming eight nuclei. It is very common for eight ascospores to be formed, although frequently the number is less, due to the non-functioning of one or more.

It is well known that in all the higher plants there is a double division of the spore mother cell during which the number of chromosomes is reduced. The doubling of the chromosomes occurs upon the fusion of the nuclei of the two sex cells. Since this double division is necessitated by the single fusion, Harper believes that the double nuclear fusion in the mildews, one in the oogonium and one in the ascus, necessitates a triple division in order to bring about the corresponding reduction in the number of the chromosomes. Harper also interprets the ascus as a spore mother cell.

Host Distribution. Some morphological species of the powdery mildews are limited to a single host. For example, *Podosphaera biuncinata* occurs only on *Hamamelis virginiana,* and *Uncinula geniculata* on *Morus rubra.* Others are confined to the species of a single genus of host plant, for example, *Uncinula circinata* on Acer, *Erysiphe aggregata* on Alnus. Again some occur on a number of different genera all of which belong to the same family, for example, *Erysiphe graminis* on various grasses. Several

of the mildews, however, have a very wide range of hosts. Perhaps the most striking cases are *Erysiphe polygoni* on 355 hosts belonging to 42 families, *E. cichoracearum* on 280 hosts belonging to 27 families and *Phyllactinia corylea* on 144 hosts belonging to 36 families.

Several cases are known where two or more different species of mildews occur on the same host. These may have the same or a different geographical distribution. For example, *Microsphaera alni* and *Phyllactinia corylea* both occur on the common hazelnut, *Corylus americana; Erysiphe polygoni* and *Microsphaera alni* occur on *Lathyrus venosus;* and three different mildews, *Sphaerotheca mors-uvae, Microsphaera grossulariae* and *Phyllactinia corylea* have been reported on *Ribes Grossularia.*

Biologic Specialization. In recent years a great deal of experimental work has been done to determine whether a mildew growing on one host can produce infection on another plant which is known to be infected by the same morphological species. Neger (39) was the first to show that some of the morphological species of mildews are broken up into biologic forms, limited to definite host plants. Marchal (35-36), Reed (45-49), Salmon (52-57), Steiner (63), and Voglino (68), have very greatly extended our knowledge regarding the biological specialization of different mildews.

Thus far one or more species of five genera-Uncinula, Erysiphe, Microsphaera, Phyllactinia and Sphaerotheca—have been tested for host specialization, no results as yet having been recorded for Podosphaera. Most of the data obtained, however, are very incomplete except possibly in the case of three species of Erysiphe, namely *E. Polygoni, E. cichoracearum* and *E. graminis,* and one species of *Sphaerotheca, Sph. humuli.*

The grass mildew, *Erysiphe graminis,* has proven to be exceptionally favorable for studies on biologic specialization. The result has been the discovery of a large number of facts bearing upon this problem. As already noted this morphological species occurs on approximately sixty different grasses. So far, however, the work indicates that in practically every case the biologic forms are restricted to the species of a single genus. For example, conidia from wheat will not infect barley, oats nor rye; conidia from barley

will not infect wheat, oats nor rye. In other words, in every case the mildew on one cereal is unable to pass over onto the species of other cereals.

Not all species of a particular genus, however, may be susceptible to the mildew. For example, the mildew on barley will infect the common barley and also *Hordeum decipiens, H. hexastichon, H. intermedium, H. bulbosum, H. distichum, H. maritinum* and *H. zeocriton,* but will not pass over onto *H. jubatum, H. murinum, H. secalinum nor H. sylvaticum.* Young plants of *Hordeum nodosum* are easily infected with the barley mildew but older plants are immune. A similar case has been found by Salmon (56) among the brome grasses. As a result of his work upon the mildews of the brome grasses, Salmon believes that there are four or perhaps five biologic forms within this one genus alone.

The wheat mildew, while able to pass over onto one or more varieties of every species of Triticum tested, is not capable of infecting all of the varieties of wheats. In a recent paper (49) I published the results of tests with seventy-eight varieties distributed among nine different species of this genus. Of these seventy-eight varieties four proved to be immune, two belonging to *T. dicoccum* and two to *T. vulgare.* In a few other cases the percentage of infection was rather low but in a great majority of cases the percentage of infection approached 100.

In some unpublished results I have been able to transfer the wheat mildew to different species of Aegilops. Several species were tested and nearly all of them proved highly susceptible. If Aegilops is to be regarded as a distinct genus as some systematists believe, we have a case of one biological form of grass mildew occurring on the species of two different genera. A similar relation is found in the case of the oat mildew, for I have been able to confirm Marchal's statement that the conidia from oats are able to infect seedlings of *Arrhenatherum elatius,* although the percentage of infection is not very high.

Well developed biologic forms have been found on other grasses. The mildew on species of Agropyron are confined to the hosts of this genus. Similarly the orchard grass mildew is confined to *Dactylis glomerata* and the blue grass mildew to species of Poa.

In addition to the grass mildew very full results have been obtained with *Erysiphe cichoracearum*. As already noted, this mildew occurs upon 280 hosts belonging to 27 families. It is therefore a very cosmopolitan species. The results indicate, however, that it is broken up into biologic forms. I (47) have found that distinct forms occur on cucurbits, asters and golden rods. I have also found that the cucurbit mildew occurs on at least eleven species of cucurbits belonging to seven genera. Six other species were also slightly infected. In fact only three species of cucurbits tested remained entirely resistant to the mildew. I further found that plants of *Plantago rugelii* and of *Helianthus annuus* could be infected by the mildew growing upon the cucurbits. In this case therefore this biologic form not only occurs on several genera of a single family but even passes out beyond the limits of the family.

Salmon (56) in his work on the mildew of the brome grasses, and Steiner (63) more recently in his work with the mildew of Alchemilla, have described what they call "bridging species." Salmon found that the mildew on *Bromus racemosus* failed to infect *B. commutatus* (twelve trials), while it infected *B. hordeaceus* in one hundred per cent of the cases (thirty-four trials). Furthermore, conidia from *B. commutatus* failed to infect *B. racemosus* (thirty-six trials), while the mildew occurring in nature on *B. hordeaceus* infected *B. commutatus* (forty out of forty-nine trials). From these data, Salmon concludes that *B. hordeaceus* may act as a "bridge" for the mildews on *B. racemosus* and *B. commutatus*. Salmon tested this in one case by infecting *B. hordeaceus* with conidia from *B. racemosus*. The conidia produced on the former were then used to infect *B. commutatus*. Similarly Steiner regards *Alchemilla pastoralis* as a "bridge" for *Sphærotheca humuli* to pass from *A. connivens* to *A. micans*.

The question of the degree of biologic specialization in other mildews is one of great interest and one which can be attacked with relative ease. There are many cases of peculiar host distribution which should be investigated from the physiological standpoint. For example, *Microsphaera diffusa* is reported by Salmon in his monograph as occurring on twelve herbaceous legumes and three species of *Symphoricarpos*, a shrubby plant belonging to the Caprifoliaceæ.

To be sure a distinct species, based on morphological characters, is recognized by some as occurring on Symphoricarpos. Infection experiments would determine whether the mildew on the legumes is transferable to Symphoricarpos or not and might indicate whether the minor morphological differences are of sufficient importance to regard the form on Symphoricarpos as a distinct species.

It is further of interest that *Phyllactinia corylea* occurs on such a wide range of hosts and that the one species of the genus has a world wide distribution. While certain workers have described other species of the genus yet the great morphological similarity of this mildew on its various hosts is very striking. Voglino (68) has found some evidence for biologic specilization in this mildew.

Economic Importance. The mildews are obligate parasites and as such frequently cause a great deal of injury to their hosts. While as a general rule these fungi are not considered as destructive as the rusts and smuts, still there are many plants of economic importance that are seriously attacked by some species of powdery mildew.

The powdery mildew of the grape, *Uncinula necator,* has for a long time been recognized as a serious menace to the culture of grapes in various parts of Europe. In 1847 Berkeley (7) reported that "the grapes in the neighborhood of Margate (England) have for the past two years been attacked by a peculiar mildew of a most destructive character." Very soon after this the disease was reported from the vineyards of southern France and other European countries, causing destruction to the grape harvest.

The American gooseberry mildew, *Sphaerotheca mors-uvae,* has proven very destructive to the English varieties of gooseberries, so that their cultivation in this country is attended with great loss. The fungus attacks especially the fruit, covering the berries with a close felt-like mycelium. The mycelium becomes dark colored and thick-walled with age and the perithecia are imbedded in it. In recent years (21, 58) the mildew has occurred in epidemic form in England and other European countries. Its appearance everywhere has occasioned great loss to growers of gooseberries, not only by destroying the year's crop of fruit but also by weakening the bushes themselves through injury to twigs and leaves. It is interesting to

note that the European gooseberry mildew, *Microsphaera grossulariæ,* is not ordinarily troublesome although injury has been reported, the affected leaves becoming shrivelled and falling prematurely.

The rose mildew, *Sphaerotheca pannosa,* is often very destructive to roses. While especially likely to attack roses cultivated in the greenhouse, the fungus also attacks certain varieties in the garden. The crimson rambler is notably susceptible, for the fungus develops on the young leaves causing these to curl and arch; the young stems are also attacked and more or less deformed. It also attacks the flower buds forming a white mealy growth and blasting the flowers. The conidia are formed in great abundance and the disease spreads very rapidly.

The hop, in many regions, suffers serious injury from the spread of the hop mildew, *Sphaerotheca humuli.* The worst damage is done when the disease attacks the cones causing them to shrivel up. In some parts of England this disease is much dreaded by the hop growers. Comparatively recently the hop mildew has become serious in the hop yards of New York (9). In some counties the entire hop crop has been ruined by the ravages of this fungus while in others the yield has been decreased and the quality of the crop much impaired.

Among other plants that are sometimes seriously attacked by the mildews the following may be mentioned: Grasses are sometimes seriously injured by the spread of *Erysiphe graminis.* Anderson (2) reports that this mildew in the northwestern states "affects chiefly the Poas and is especially damaging to *P. tenuiflora,* one of our most valued forage grasses." Stewart (64) has reported the occurrence of the mildew on wheat in the spring but, although the disease spreads very rapidly, no serious permanent injury to the wheat crop results. Cucumbers when forced in the greenhouse are sometimes severely attacked by *Erysiphe cichoracearum.* Nursery stock, as apples, peaches and cherries, are frequently damaged by powdery mildews.

As a general rule it is not difficult to control the outbreaks of diseases due to powdery mildews. Repeated experience has shown that flowers of sulphur, dusted on the infected plants, is a satisfac-

tory remedy. Most of the mildews seem to be controlled by this treatment, especially when prompt measures are taken at the first indication of an outbreak. A relatively strong solution of potassium sulphide—one ounce in two gallons of water—is also effective in the treatment of some diseases caused by mildew.

Pathological Effects. As a general thing the mildews do not cause any striking pathological changes in the cells of the host. Ordinarily no appreciable malformation occurs or hypertrophy. However, an enlargement of the twigs of Physocarpus, similar to Witches' Brooms, are produced by the development of *Sphaerotheca humuli.*

One effect of some of these mildews is very striking. When Maple leaves infected with *Uncinula circinata* are collected in the late fall they will be found to show characteristic yellow and green areas. Examination shows that the green areas are infected with the mildew. The infected host cells are stimulated to retain their green color longer than the other cells of the leaf. A similar effect may be seen on grass leaves when badly covered with the mildew. The results may be made more striking by placing leaves of barley, for example, in a moist glass chamber and inoculating with conidia from barley. In three to four days numerous infected areas will be distinctly visible and possess a deep green color while the other portions of the leaves will be a pale yellow.

Collection, Preservation and Cultivation of the Powdery Mildews. The powdery mildews are usually conspicuous objects on leaves and other parts of living plants. Sometimes careful search is needed to locate the perithecia. When hunting for mildews one needs to examine both surfaces of the leaves for many forms occur mainly or entirely on the under surface of leaves. This is particularly true of *Phyllactinia corylea.*

Special care, of course, must be taken to properly identify the host plant. In fact it is generally a good plan to collect flowering or fruiting parts of the host and keep these with the infected leaves.

For the systematic study of the powdery mildews dry material is very satisfactory. Infected parts of plants are collected and

placed between driers for a few days. The material is then transferred to suitable envelopes, properly labeled, and laid aside for future study.

Many of the mildews are easily cultivated in greenhouses and afford exceptionally fine material for the study of various problems. In general a succession of crops of young hosts must be provided so that the mildew will be able to spread over on to the young plants. The grass mildew on various hosts, when once secured, may easily be propagated by planting additional seed of the proper hosts at intervals of one to four weeks. Various other mildews are also readily propagated in a similar manner. The writer has successfully cultured for long periods the mildews on cucurbits, goldenrod, aster, Erigeron, apple, sunflower, various cereals and grasses, etc. As pointed out by Melhus (37) the sunflower mildew is particularly favorable for class use because of the readiness with which perithecia appear upon the host.

The writer has experienced a great deal of difficulty in propagating the mildews during the summer months. The high temperature of the greenhouse seems to be the controlling factor. The mildew, however, is especially infested by thrips, a small insect which seems to spread very rapidly during the summer season.

Classification. The powdery mildews have long been an object of study from the systematic standpoint. Practically all of the earlier mycological workers have devoted more or less attention to the group. Probably the first mention made of one of these fungi was by Linnaeus in *Species Plantarum* (1753) under the name of *Mucor Erysiphe*. Following Linnaeus, Persoon (42, 43), Rebentisch (44), (who published the first illustration), de Candolle (13), Fries (24), and others made additions to our knowledge of mildews. The most important papers dealing with the systematic arrangement of these fungi are those by Wallroth (69, 70) (1819) who insisted upon the distinction of species on the basis of morphological characters and not by the host plant upon which they grew; by Schweinitz (60) (1834), who described several North American forms; by Léveillé (33) (1851), who divided the group into six genera, based upon the number of asci in the perithecium and the characters of the appendages, the names and limits of these genera

being retained to the present day; by the Tulasne brothers (66) (1861), who described and very fully illustrated by exceptionally fine copper plates sixteen species, although they placed them all under one genus—Erysiphe; by Cooke & Peck (14) (1872) who listed the mildews of the United States; by Burrill (12) (1892) who described the North American forms then known; by Salmon (50) (1900) who has monographed the group with exceptional completeness and whose work is the standard at the present time.

Many lists from various states have also been published. These give us much desired information regarding the occurrence and distribution of the mildews in the United States. Among the more important of these state lists the following may be mentioned: Anderson (Iowa) (1), Anderson (Montana) (2, 3), Atkinson (Carolina and Alabama) (4), Brannon (Indiana) (10), Burrill and Earle (Illinois) (11), Davis (Wisconsin) (17, 18, 19, 20), Farlow (Massachusetts) (22), Freeman (Minnesota) (23), Griffiths (northwestern states) (26), Harkness and Moore (California) (27), Lawrence (Washington) (32), Millspaugh and Nuttall (West Virginia) (38), Selby (Ohio) (61), Tracy and Earle (Mississippi) (65), Underwood and Earle (Alabama) (67), Walters (Kansas) (71).

In the following classification of the *Erysiphaceæ* Salmon (50, 51) is largely followed. Most of the facts stated are taken from his monograph and supplementary notes.

Salmon in his monograph (50) recognizes six genera, forty-nine species and eleven varieties.

Saccardo on the contrary recognizes a much larger number of species. Of Salmon's species and varieties, thirty-one species and seven varieties are found in North America. Of these thirteen species and five varieties have been reported only from this continent.

Some interesting cases of distribution may be noted. The maple mildew of North America is *Uncinula circinata,* while a different species, *A. aceris* is reported on the maples of Europe. *Sphaerotheca morse-uvae* in North America specially attacks species of Ribes; in Europe this same form is reported on species of Euphorbia. Very recently, as already noted, this mildew has also appeared on Ribes

in Europe, but it is thought to have been introduced from America. *Microsphaera alni* is very common on the lilac, *Syringa vulgaris,* in this country, but according to Magnus (34) is not found on this host in Europe, although the fungus on other hosts is quite common.

Following Léveillé, Salmon divides the Erysiphaceæ into six genera[1] and uses the same generic names as proposed by Léveillé. The following keys, which are based on Salmon's monograph and which are quite generally used in this or in slightly different form, may serve to differentiate the genera and species.

Key to Genera

A. Perithecium containing a single ascus B.
  B. Appendages unbranched, more or less flexuous, arising from the base of the perithecium.................................*Sphærotheca.*
  B. Appendages one to several times dichotomously branched at the apex ....*Podosphæra.*
A. Perithecium containing several asci C.
  C. Appendages without bulbous enlargement at the base D.
    D. Appendages generally straight, dichotomously branched at the apex .... *Microsphæra.*
    D. Appendages simple, uncinate or spirally inrolled at the apex. ....*Uncinula.*
    D. Appendages simple or irregularly branched, more or less flexuous, usually somewhat similar to the mycelial hyphæ, not dichotomously branched nor uncinate at the apex....*Erysiphe.*
  C. Appendages simple, straight, rigid, with a bulbous enlargement at the base ....*Phyllactinia.*

Sphaerotheca Léveillé. (Plate XVI, Figs. 38, 38a)

The perithecia are subglobose, containing a single ascus which is regularly 8-spored. The appendages are flexuous, brown or colorless, spreading horizontally and often interwoven with the mycelium which they frequently resemble; they are simple or rarely branched, sometimes lacking.

Sphærotheca is represented by five species and one variety, all of which have been reported from the United States.

1. Salmon (59) has since placed *Erysiphe taurica* in a new genus by itself—Oidiopsis—making in all seven genera.

Key to Species

A. Mycelium persistent, thick, pannose, forming dense patches composed of special hyphæ, in which the perithecia are more or less immersed B.
- B. Persistent mycelium usually satiny and shining, white, sometimes becoming gray or pale brown............*S. pannosa* (Wallr.) Lév.
- B. Persistent mycelium dark brown C.
  - C. Inner wall of the perithecium separating from the outer; hyphæ of persistent mycelium very tortuous......*S. lanestris* Harkn.
  - C. Inner wall not separating, hyphae straighter............... ....*S. mors-uvae* (Schw.) B. & C.

A Mycelium without these characters D.
- D. Perithecia 60-78μ in diameter, ascus 60-75x42-50μ; inner wall of perithecium separating from the outer..*S. phytoptophila* K. & S.
- D. Perithecia 50-120μ in diameter, ascus 45-90x50-72μ; inner wall scarcely separating from the outer E.
  - E. Cells of outer wall of perithecium 10-20μ wide, averaging 15μ ....*S. humuli* (DC.) Burrill.
  - E. Cells of outer wall of perithecium 20-30 (rarely 40)μ wide, averaging 25μ......*S. humuli* var. *fuliginea* (Schlecht.) Salm.

Hosts:

Sphærotheca pannosa; Rosa (various species).
S. lanestris: *Quercus agrifolia, Q. alba, Q. macrocarpa.*
S. mors-uvæ: *Ribes* (various species).
S. phytoptophila: *Celtis occidentalis.*
S. humuli: *Agrimonia striata, Geranium maculatum, Geum canadense, Physocarpus opulifolius.*
S. humuli var. *fuliginea*: *Bidens chrysanthemoides, B. frondosa, Erigeron annuus, Taraxacum officinale.*

Podosphæra Kunze. (Plate XVI, Figs. 34, 34a).

Perithecia globose, or globose-depressed, containing a single ascus which is 8-spored. The appendages are equatorial or apical, dark brown or colorless, dichotomously branched at the apex, ultimate branches simple and straight or swollen and knob-shaped.

The genus contains four species and one variety, all, except one species, being represented in the United States.

Key to Species

A. Basal appendages present in addition to the apical, the latter usually unbranched.................*P. leucotricha* (Ell. & Everh.) Salm.

A. No basal appendages present B.

B. Appendages arising from near the apex of the perithecium, somewhat erect and fasciculate, one to eight times the diameter of the perithecium, dark brown for more than half their length ....*P. oxyacanthæ* var. *tridactyla* (Wallr.) Salm.
B. Appendages equatorially inserted and more or less spreading C.
  C. Appendages colorless, or faintly tinged with brown at the base, branched apex not swollen.............*P. biuncinata* C. & P.
  C. Appendages dark brown for more than half their length, ultimate branches of the apex knob-shaped.....................
......................................P. *oxyacanthæ* (DC.) De Bary.

Hosts:

P. leucotricha: *Pyrus malus.*
P. biuncinata: *Hamamelis virginiana.*
P. oxyacanthæ: *Prunus* (various species).
P. oxyacanthæ var. *tridactyla*[1]: *Spiræa Douglasii.*

UNCINULA Léveillé. (Plate XVI, Figs. 37, 37a).

This genus is easily distinguished by the uncinate apex of the appendages. The perithecia are globose or globose-depressed and contain several asci, two to eight spored. The appendages are simple in all American forms.

There are eighteen species and two varieties. Of these ten species occur in the United States.

Key to Species

A. Appendages colored for half their length or more....................
....*U. necator* (Schw.) Burrill.
A. Appendages colorless B.
  B. Asci containing 2-3 spores C.
    C. Perithecia very large 215-320μ in diameter; more than 30 asci in the perithecium............*U. polychaeta* (B. & C.) Ellis
    C. Perithecia averaging 130μ; asci 8-20 in the perithecium....
    ....*U. macrospora* Peck.
  B. Asci containing 4-8 spores D.
    D. Appendages delicate, narrow, 3-4μ wide; asci 4-7 spored E.
      E. Perithecia 150-200μ in diameter; asci about 25.............
      ....*U. confusa* Massee.
      E. Perithecia 86-122μ in diameter; asci 5-8 G.
        G. Appendages 50-160, ½-¾ times the diameter of perithecium.............................*U. parvula* C. & P.

1. Reported only from Washington.

G. Appendages 24-46, 1½-2 times the diameter of perithecium, often geniculate..................*U. geniculata* Gerard.

D. Appendages stouter, wider, or if narrow with asci 8-spored F.

F. Appendages abruptly flexuose, about equalling the diameter of perithecium, spores usually 8...............*U. flexuosa* Peck.

F. Appendages all straight H.

H. Appendages thick walled, refractive or rough at base, perithecia 64-146μ in diameter............*U. clintonii* Peck.

H. Appendages thin walled throughout I.

I. Perithecia 90-175μ in diameter, averaging 135μ; asci containing 4-6 spores..........*U. salicis* (DC.) Winter.

I. Perithecia 160-225μ in diameter, averaging 190μ; asci containing 7-8 spores...........*U. circinata* C. & P.

Hosts:

Uncinula necator: *Psedera quinquefolia, Vitis* (various species).
U. polychaeta[1]: *Celtis occidentalis.*
U. macrospora: *Ulmus americana, U. fulva.*
U. confusa[2]: *Celtis occidentalis.*
U. parvula: *Celtis occidentalis.*
U. geniculata: *Morus rubra.*
U. flexuosa: *Aesculus glabra.*
U. clintonii: *Tilia americana.*
U. salicis: *Populus* (various species), *Salix* (various species).
U. circinata: *Acer saccharinum.*

Erysiphe Hedw. (Plate XVI. Figs. 36, 36a).

Perithecia are generally globose and contain several asci, 2-8 spored. Appendages are floccose, simple or irregularly branched, never with a definite apical branching, sometimes obsolete, usually more or less similar to the mycelium and interwoven with it.

The genus contains eight species and one variety of which seven species and the variety occur in the United States.

Key to Species

A. Perithecia large, 135-280μ in diameter, averaging 200μ B.

B. Perithecia immersed in a lanuginose persistent mycelium; asci not containing spores on the living host..............*E. graminis* DC

B. Perithecia not immersed in a lanuginose persistent mycelium; asci containing spores on the living host C.

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1. Reported only from S. Carolina, Alabama and Mississippi.
2. Never found but once and then associated with *U. parvula*.

C. Asci containing eight spores, rarely six or seven; spores somewhat spherical, 16-20x10-15μ.....*E. aggregata* (Peck) Farlow.

C. Asci containing four to six spores; spores 20-22x10-12μ...... ....*E. polygoni* var. *sepulta* (Ell. & Everh.) Salm.

C. Asci containing two spores; spores 28-40x18-22μ; perithecia at maturity becoming cup-shaped.................*E. taurica* Lév.

A. Perithecia smaller, 65-180μ, not immersed in a lanuginose mycelium D.

D. Asci not containing spores on the living host; haustoria lobed.... ....*E. galeopsidis* DC

D. Asci generally containing spores on the living host; haustoria not lobed E.

E. Perithecia containing 4-25 asci, usually 10-15; asci 58-90x30-50μ; spores generally two, 20-28x12-20μ......*E. cichoracearum* DC.

E. Perithecia containing few asci, 2-8, rarely as many as 22; asci 46-72x30-45μ; spores 3-8, rarely 2, 19-25x9-14μ.*E. polygoni* DC.

A. Perithecia small, 52-60μ in diameter, containing usually three asci; asci 48-50x28-36μ; asci two, rarely three, spored......*E. trina* Harkn.

Hosts:

Erysiphe graminis: *Agropyron repens, Avena sativa, Dactylis glomerata, Hordeum vulgare, Poa pratensis, Secale cereale, Triticum vulgare.*

E. aggregata: *Alnus incana* (catkins).

E. galeopsidis: *Scutellaria latifolia, Stachys tenuifolia.*

E. polygoni: *Astragalus canadensis, Clematis virginiana, Lathyrus venosus, Polygonum aviculare, Ranunculus abortivus.*

E. polygoni var. *sepulta*:[1] *Bigelovia graveolens.*

E. cichoracearum: *Actinomeris alternifolia, Ambrosia trifida, Aster cordifolius, A. laevis, A. sagittifolius, Eupatorium purpureum, Helianthus annuus, Cucumis sativus, Cucurbita maxima, Solidago canadensis.*

E. trina[2]: *Quercus agrifolia.*

E. taurica[3]: *Heliopsis scabra.*

MICROSPHÆRA Léveillé. (Plate XVI. Figs. 39, 39a).

The perithecia are globose to globose-depressed and contain several asci, 2-8 spored. The appendages are not interwoven with the mycelium; they are divided several times in a dichotomous manner at the apex.

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1. Reported from Rocky Mountain States.
2. Reported only from California.
3. Reported by Salmon as an old world species but recorded by Anderson (1) from Iowa.

The genus is represented by thirteen species and six varieties of which five species and four varieties occur in North America.

Key to Species

A. Appendages 2½-7 times the diameter of the perithecia, usually much contorted and angularly bent; apical branching of appendages very irregular and lax, with the branches flexuous and more or less curled.............................. *M. euphorbiæ* (Peck) B. & C.

A. Appendages long or short without above characters B.

- B. Tips of some or all of the ultimate branches of the appendages recurved C.
  - C. Appendages long and flaccid D.
    - D. Apex of appendages much branched, ornate, more or less close; spores 22-26x12-15μ.. *M. alni* var. *extensa* (C. & P.) Salm.
    - D. Apex of appendages less branched, more or less widely forked, or branching close and simple; spores 18-23x9-13μ .... *M. alni* var. *vaccinii* (Schw.) Salm.
  - C. Appendages short, not exceeding 2½ times the diameter of the perithecium E.
    - E. Appendages more or less contorted, apical branching very lax and irregular.............. *M. alni* var. *ludens* Salm.
    - E. Appendages not contorted, apical branching closer and regular; tips regular, recurved F.
      - F. Axis of some appendages not dividing dichotomously at the apex, but bearing sets of opposite branches.... .... *M. alni* var *calocladophora* (Atk.) Salm.
      - F. Appendages regularly dichotomous at apex........... .... *M. alni* (Wallr.) Salm.
- B. Tips of appendages not recurved G.
  - G. Appendages 3-7 times diameter of perithecia; colored, nearly to apex................................. *M. Russellii* Clinton.
  - G. Appendages colorless H.
    - H. Branching of appendages lax, irregular; ultimate branches long, forming a narrow fork.......... *M. diffusa* C. & P.
    - H. Branching closer and more regular; apex of appendages with very short primary and secondary branches, more or less digitate............ *M. grossulariæ* (Wallr.) Lev.

Hosts:

M. euphorbiae: *Euphorbia corallata.*

M. alni: *Gleditsia triacanthos, Lathyrus odoratus, Platanus occidentalis, Syringa vulgaris, Viburnum Lentago.*

M. alni var. *vaccinii*: *Vaccinium* (various species).

M. alni var. *ludens*[1]: *Vicia americana.*
M. alni var. *extensa*: *Quercus* (various species).
M. alni var. *calocladophora*[2]: *Quercus aquatica.*
M. Russellii: *Oxalis stricta.*
M. diffusa: *Desmodium canadense, Lespedeza capitata, Symphoricarpos orbiculatus.*
M. grossulariæ: *Ribes nigrum, Sambucus canadensis.*

PHYLLACTINIA Léveillé. (Plate XVI. Figs. 35, 35a).

This genus is easily recognized by the large (140-270μ in diam.) globose-depressed perithecia with the equatorial rigid, colorless, acicular appendages with a bulbous swelling at the base. The perithecia contain many asci which are regularly 2-spored, rarely 3-spored. The apex of the perithecium is provided with numerous crowded, branched penicillate cells which arise from the outer cells of the perithecial wall.

The mycelium of this genus is characteristically internal, developing in the intercellular spaces of the leaf. Special branches, haustoria, penetrate into the cells of the spongy parenchyma.

This genus is widely distributed and is represented by a single species—*Phyllactinia corylea* (Pers.) Karst.

Hosts:

Betula alba, Celastrus scandens, Cornus stolonifera, Corylus Americana, Ostrya virginiana.

Host Index. The following list includes about one hundred and seventy-five hosts of the Erysiphaceæ. The list is by no means intended as a complete one of the powdery mildews of the United States, but it does include the common hosts, most of which have a wide distribution and upon which the various species of mildews may be found. Collections of nearly all of these are found in the herbarium of the writer. A few are taken from the records of different state lists. In naming the hosts, Gray's New Manual of Botany, revised by Robinson and Fernald, is strictly followed.

1. Reported only from S. Dakota and Montana.
2. Reported only from S. Carolina, Alabama and Mississippi.

Host	Fungus
Acer rubrum L.	Uncinula circinata C. & P.
Acer saccharum Marsh.	Uncinula circinata C. & P.
Acer saccharinum L.	Uncinula circinata C. & P.
Actinomeris alternifolia (L.) DC.	Erysiphe cichoracearum DC.
Aesculus glabra Willd.	Uncinula flexuosa Peck.
Agrimonia striata Michx.	Sphærotheca humuli (DC.) Burr.
Agropyron repens (L.) Beauv.	Erysiphe graminis DC.
Alnus incana (L.) Moench.	Erysiphe aggregata (Peck) Farl.
Ambrosia artemisifolia L.	Erysiphe cichoracearum DC.
Ambrosia trifida L.	Erysiphe cichoracearum DC.
Amphicarpa monoica (L.) Ell.	Erysiphe polygoni DC.
Apios tuberosa Moench.	Microsphæra diffusa C. & P.
Aquilegia canadensis L.	Erysiphe polygoni DC.
Aquilegia coerulea James.	Erysiphe polygoni DC.
Aster cordifolius L.	Erysiphe cichoracearum DC.
Aster laevis L.	Erysiphe cichoracearum DC.
Aster paniculatus Lam.	Erysiphe cichoracearum DC.
Aster puniceus L.	Erysiphe cichoracearum DC.
Aster sagittifolius Wedemeyer.	Erysiphe cichoracearum DC.
Aster Tradescanti L.	Erysiphe cichoracearum DC.
Astragalus canadensis L.	Erysiphe polygoni DC.
Avena sativa L.	Erysiphe graminis DC.
Betula alba L. var. papyrifera (Marsh) Spach.	Phyllactinia corylea (Pers.) Karst.
Bidens cernua L.	Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Bidens lævis (L.) BSP.	Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Bidens frondosa L.	Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Bigelovia graveolens A. Gray.	Erysiphe polygoni DC. var. sepulta (E. & E.) Salm.
Carpinus caroliniana Walt.	Microsphæra alni (Wallr.) Salm.
Castanea dentata (Marsh.) Borkh.	Microsphæra alni (Wallr.) Salm.
Catalpa speciosa Warder.	Microsphæra alni (Wallr.) Salm. var. vaccinii (Schw.) Salm.
Ceanothus americanus L.	Microsphæra alni (Wallr.) Salm.
Celastrus scandens L.	Phyllactinia corylea (Pers.) Karst.
Celtis occidentalis L.	Sphærotheca phytoptophila K. & S.
Celtis occidentalis L.	Uncinula polychæta (B. & C.) Ellis
Celtis occidentalis L.	Uncinula parvula C. & P.
Chelone glabra L.	Erysiphe galeopsidis DC.
Cirsium lanceolatum (L.) Hill.	Erysiphe cichoracearum DC.
Cirsium muticum Michx.	Erysiphe cichoracearum DC.

Clematis virginiana L................ Erysiphe polygoni DC.
Cornus alternifolia L. f.............. Microsphæra alni (Wallr.) Salm.
Cornus stolonifera Michx............. Phyllactinia corylea (Pers.) Karst.
Corylus americana Walt.............. Microsphæra alni (Wallr.) Salm.
Corylus americana Walt.............. Phyllactinia corylea (Pers.) Karst.
Cratægus Crus-galli L............... Podosphæra oxyacanthæ (DC) de B.
Cratægus coccinea L................. Podosphæra oxyacanthæ (DC.) de B.
Crepis acuminata Nutt............... Erysiphe cichoracearum DC.
Cucumis sativus L................... Erysiphe cichoracearum DC.
Cucurbita maxima Duchesne......... Erysiphe cichoracearum DC.
Cucurbita Pepo L.................... Erysiphe cichoracearum DC.
Dactylis glomerata L................. Erysiphe graminis DC.
Desmodium canescens (L.) DC....... Microsphæra diffusa C. & P.
Desmodium canadense (L.) DC....... Microsphæra diffusa C. & P.
Desmodium paniculatum (L.) DC..... Microsphæra diffusa C. & P.
Elymus striatus Willd................ Erysiphe graminis DC.
Erigeron annuus (L.) Pers.......... Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Erigeron canadensis L................ Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Eupatorium urticæfolium Reichard... Erysiphe cichoracearum DC.
Eupatorium perfoliatum L............ Erysiphe cichoracearum DC.
Eupatorium purpureum L............. Erysiphe cichoracearum DC.
Euphorbia corollata L................ Microsphæra euphorbiæ (Peck) B. & C.
Euphorbia marginata Pursh.......... Microsphæra euphorbiæ (Peck) B. & C.
Fraxinus americana L................ Phyllactinia corylea (Pers.) Karst.
Fraxinus Pennsylvanica Marsh....... Phyllactinia corylea (Pers.) Karst.
Galium Aparine L.................... Erysiphe cichoracearum DC.
Geranium carolinianum L............ Sphærotheca humuli (DC.) Burr.
Geranium maculatum L............... Sphærotheca humuli (DC.) Burr.
Gerardia grandiflora Benth........... Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Geum canadense Jacq................ Sphærotheca humuli (DC.) Burr.
Gilia micrantha (Kell.) A. Nels...... Sphærotheca humuli (DC.) Burr.
Gleditsia triacanthos L.............. Microsphæra alni (Wallr.) Salm.
Grindelia squarrosa (Pursh.) Duval.. Erysiphe cichoracearum DC.
Hamamelis virginiana L.............. Podosphæra biuncinata C. & P.
Helenium autumnale L............... Erysiphe cichoracearum DC.
Helianthus annuus L................. Erysiphe cichoracearum DC.
Helianthus decapetalus L............ Erysiphe cichoracearum DC.
Helianthus strumosus L.............. Erysiphe cichoracearum DC.
Helianthus tuberosus L............... Erysiphe cichoracearum DC.
Heliopsis scabra Duval............... Erysiphe taurica Lév.

Hordeum vulgare L.	Erysiphe graminis DC.
Humulus Lupulus L.	Sphærotheca humuli (DC.) Burr.
Hydrophyllum appendiculatum Michx.	Erysiphe cichoracearum DC.
Hydrophyllum macrophyllum Nutt.	Erysiphe cichoracearum DC.
Inula Helenium L.	Erysiphe cichoracearum DC.
Lathyrus ochroleucus Hook.	Microsphæra alni (Wallr.) Salm.
Lathyrus odoratus L.	Microsphæra alni (Wallr.) Salm.
Lathyrus palustris L.	Microsphæra alni (Wallr.) Salm.
Lathyrus venosus Muhl.	Erysiphe polygoni DC.
Lespedeza capitata Michx.	Microsphæra diffusa C. & P.
Ligustrum vulgare L.	Microsphæra alni (Wallr.) Salm.
Lonicera sempervirens L.	Microsphæra alni (Wallr.) Salm.
Lonicera tartarica L.	Microsphæra alni (Wallr.) Salm.
Lupinus perennis L.	Erysiphe polygoni DC.
Morus rubra L.	Uncinula geniculata Gerard.
Oenothera biennis L.	Erysiphe polygoni DC.
Ostrya virginiana (Mill.) K. Koch.	Microsphæra alni (Wallr.) Salm.
Ostrya virginiana.	Phyllactinia corylea (Pers.) Karst.
Oxalis stricta L.	Microsphæra Russellii Clinton.
Parietaria Pennsylvanica Muhl.	Erysiphe cichoracearum DC.
Parnassia caroliniana Michx.	Erysiphe polygoni DC.
Phlox paniculata L.	Erysiphe cichoracearum DC.
Physocarpus opulifolius (L.) Maxim.	Sphærotheca humuli (DC.) Burr.
Pisum sativum L.	Erysiphe polygoni DC.
Plantago major L.	Erysiphe cichoracearum DC.
Plantago Rugellii Dcne.	Erysiphe cichoracearum DC.
Platanus occidentalis L.	Microsphæra alni (Wallr.) Salm.
Poa pratensis L.	Erysiphe graminis DC.
Polygonum aviculare L.	Erysiphe polygoni DC.
Polygonum erectum L.	Erysiphe polygoni DC.
Polygonum exsertum Small.	Erysiphe polygoni DC.
Polygonum scandens L.	Erysiphe polygoni DC.
Populus deltoides Marsh.	Uncinula salicis (DC.) Winter.
Populus grandidentata Michx.	Uncinula salicis (DC.) Winter.
Populus tremuloides Michx.	Uncinula salicis (DC.) Winter.
Prunus Besseyi Bailey.	Podosphæra oxyacanthæ (DC.) de B.
Prunus (cultivated cherry & plum).	Podosphæra oxyacanthæ (DC.) de B.
Psedera quinquefolia (L.) Greene.	Uncinula necator (Schw.) Burr.
Pyrus malus L.	Podosphæra leucotricha (E. & C.) Salm.
Quercus alba L.	Microsphæra alni (Wallr.) Salm.
Quercus alba L.	Sphærotheca lanestris Harkn.
Quercus agrifolia Née.	Erysiphe trina Harkn.
Quercus agrifolia Née.	Sphærotheca lanestris Harkn.

Quercus aquatica Walt............... Microsphæra alni (Wallr.) Salm. var. calocladophora (Atk.) Salm.
Quercus macrocarpa Michx.......... Sphærotheca lanestris Harkn.
Quercus macrocarpa Michx.......... Microsphæra alni (Wallr.) Salm.
Quercus Muhlenbergii Engelm........ Microsphæra alni (Wallr.) Salm.
Quercus pedunculata Ehrh. var. fastigiata DC.......................... Microsphæra alni (Wallr.) Salm.
Quercus Prinus L.................... Microsphæra alni (Wallr.) Salm. var. extensa (C. & P.) Salm.
Quercus rubra L..................... Microsphæra alni (Wallr.) Salm. var. extensa (C. & P.) (Salm.)
Quercus velutina Lam................ Microsphæra alni (Wallr.) Salm. var. extensa (C. & P.) (Salm.)
Ranunculus abortivus L.............. Erysiphe polygoni DC.
Ranunculus acris L................... Erysiphe polygoni DC.
Rhus glabra L........................ Sphærotheca humuli (DC.) Burr.
Rhus typhina L....................... Sphærotheca humuli (DC.) Burr.
Ribes Grossularia L.................. Sphærotheca mors-uvae (Schw.) B. & C.
Ribes nigrum L...................... Microsphæra grossulariæ (Wallr.) Lév.
Rosa (cultivated species, Crimson Rambler) .... Sphærotheca pannosa (Wallr.) Lév.
Rubus hispidus L.................... Sphærotheca humuli (DC.) Burr.
Salix cordata Muhl.................. Uncinula salicis (DC.) Winter.
Salix discolor Muhl................. Uncinula salicis (DC.) Winter.
Salix nigra Marsh................... Uncinula salicis (DC.) Winter.
Sambucus canadensis L.............. Microsphæra grossulariæ (Wallr.) Lév.
Scutellaria lateriflora L............. Erysiphe galeopsidis DC.
Shepherdia argentea (L.) Nutt....... Sphærotheca humuli (DC.) Burr.
Sicyos angulatus L.................... Erysiphe cichoracearum DC.
Solanum carolinense L.............. Erysiphe cichoracearum DC.
Spiræa Douglasii Hook.............. Podosphæra oxyacanthæ (DC.) de B. var. tridactyla (Wallr.) Salm.
Stachys palustris L.................. Erysiphe galeopsidis DC.
Stachys tenuifolia Willd.............. Erysiphe galeopsidis DC.
Symphoricarpos orbiculatus Moench... Microsphæra diffusa C. & P.
Syringa vulgaris L................... Microsphæra alni (Wallr.) Salm.
Taraxacum dumetorum Greene....... Sphærotheca humuli (DC.) Burr.
Taraxacum officinale Weber.......... Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Teucrium canadense L............... Erysiphe galeopsidis DC.
Tilia americana L.................... Uncinula clintonii Peck.
Trifolium pratense L................ Erysiphe polygoni DC.
Triticum vulgare Vill................ Erysiphe graminis DC.

Troximon parviflorum Nutt	Sphærotheca humuli (DC.) Burr. var. fuliginea (Schlecht.) Salm.
Ulmus fulva Michx	Microsphæra alni (Wallr.) Salm.
Ulmus fulva Michx	Uncinula macrospora Peck.
Vaccinium pennsylvanicum Lam	Microsphæra alni (Wallr.) Salm. var. Vaccinii (Schw.) Salm.
Valeriana edulis Nutt	Erysiphe cichoracearum DC.
Verbena hastata L	Erysiphe cichoracearum DC.
Verbena stricta Vent	Erysiphe cichoracearum DC.
Verbena urticæfolia L	Erysiphe cichoracearum DC.
Vernonia Baldwini Torr	Erysiphe cichoracearum DC.
Viburnum Lentago L	Microsphæra alni (Wallr.) Salm.
Vicia americana Muhl	Microsphæra alni (Wallr.) Salm. var. ludens Salm.
Vitis (cultivated grape)	Uncinula necator (Schw.) Burr.
Vitis cordifolia Michx	Uncinula necator (Schw.) Burr.
Vitis vulpina L	Uncinula necator (Schw.) Burr.
Zanthoxylum americanum Mill	Phyllactinia corylea (Pers.) Karst.

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EXPLANATION OF FIGURES

Figures 1-3 are copied from Smith. Figures 6, 7, 9-33 are copied from Harper. The others are from drawings made by G. T. Kline.

PLATE XIII.

Fig. 1. Haustorium of *Erysiphe polygoni* DC. on *Geranium maculatum.*

Fig. 2. Haustoria of *Uncinula salicis* (DC.) Winter on *Salix discolor.* One haustorium is located in the epidermal cell, while the other is in a subepidermal cell.

Fig. 3. Haustorium of *Erysiphe graminis* DC. on Poa.

Fig. 4. Three conidiophores of *Erysiphe graminis* DC. The characteristic enlargement at the base of the conidiophores is well shown. (Magn. 228 times).

Fig. 5. Three germinating conidia of *Erysiphe graminis* DC. (Magn. 228 times).

Fig. 6. Section through a young perithecium of *Phyllactinia corylea* (Pers.) Karst. The ascogonium of five cells is shown; the penultimate cell is budding out in ascogenous hyphæ.

Fig. 7. Median section of an older perithecium of *Phyllactinia corylea.* A portion of the ascogonium and sections of the multinucleated ascogenous hyphæ are shown.

Fig. 8. Median section of a perithecium of *Uncinula salicis.* The section shows three asci, each with the primary ascus nucleus; surrounding the asci is the inner wall composed of cells filled with dense protoplasm; outside of these the outer wall whose cells are largely devoid of protoplasmic contents and have thick walls. Four young appendages are shown.

Plate XIV.

Figs 9-20 *Sphærotheca castagnei* Lév.

Fig. 9. Oogonium and antheridial branch each containing one nucleus.

Fig. 10. Antheridial branch cut off and nucleus divided into two.

Figs. 11-12 Antheridium cut off from the stalk cell.

Fig. 13. Cell wall between antheridium and oogonium dissolved and the antheridial nucleus lying adjacent to the oogonial nucleus in the oogonium.

Fig. 14. Fusion of oogonial and antheridial nuclei; wall re-formed between antheridium and oogonium.

Fig. 15. Oogonium with fusion nucleus and surrounded by the first layer of wall cells.

Fig. 16. Oogonium surrounded by two layers of wall cells.

Fig. 17. Development of oogonium to form ascogonium. The latter now consists of two uninucleated cells.

Fig. 18. Young ascogonium with three nuclei, cell division not having occurred.

Fig. 19. Completely developed ascogonium with the cells of the inner layer of the perithecial wall shown. The penultimate cell of the ascogonium is binucleated and is the young ascus.

Fig. 20. Young ascus with the primary ascus nucleus and two ascogonium cells.

Figs. 21-24. *Phyllactinia corylea* (Pers.) Karst.

Fig. 21. Ascus with two nuclei; chromatin strands distinctly oriented with reference to the central body.

Figs. 22-24. Stages in the fusion of the two nuclei to form the primary ascus nucleus.

PLATE XV.

Figs. 25-30. *Phyllactinia corylea* (Pers.) Karst.

Fig. 25. Ascus with primary ascus nucleus.

Fig. 26. Division of primary ascus nucleus; early stage in synapsis.

Fig. 27. Division of primary ascus nucleus; loosening of chromatin following synapsis.

Fig. 28. Division of primary ascus nucleus; equatorial plate stage showing eight chromosomes, and the central bodies with the well developed asters.

Fig. 29. Binucleated ascus following completion of the first division.

Fig. 30. Second division; late anaphase stages with eight chromosomes on each half of each spindle.

Figs. 31-32 *Erysiphe cichoracearum* DC.

Fig. 31. Spore formation; plasma membrane being formed by bending back of astral rays and their fusion to form an umbrella-shaped membrane.

Fig. 32. Plasma membrane of spore about complete.

Fig. 33. *Phyllactinia corylea* (Pers.) Karst. Ascus with two spores.

PLATE XVI.

Fig. 34. Perithecium of *Podosphæra oxyacanthæ* (DC.) De Bary, on cultivated cherry. (Magn. 50 times).

Fig. 34a. Ascus of *P oxyacanthæ*. (Magn. 275 times).

Fig. 35. Perithecium of *Phyllactinia corylea* (Pers.) Karst. on *Betula alba.* (Magn. 50 times).

Fig. 35a. Ascus of *P. corylea* (magn. 275 times).

Fig. 36. Perithtecium of *Erysiphe polygoni* DC. on *Polygonum aviculare.* (Magn. 50 times).

Fig. 36a. Ascus of *E. polygoni.* (Magn. 275 times).

Fig. 37. Perithecium of *Uncinula salicis* (DC.) Winter on *Salix discolor.* (Magn. 50 times).

Fig. 37a. Ascus of *U. salicis.* (Magn. 275 times).

Fig. 38. Perithecium of *Sphærotheca Humuli* (DC.) Burr., var. *fuliginea* (Schlecht.) Salm. on *Taraxacum officinale.* (Magn. 50 times).

Fig. 38a. Ascus of *S. Humuli* var. *fuliginea.* (Magn. 275 times).

Fig. 39. Perithecium of *Microsphæra alni* (Wallr.) Salm. on *Syringa vulgaris.* (Magn. 50 times).

Fig. 39a. Ascus of *M. alni.* (Magn. 275 times).

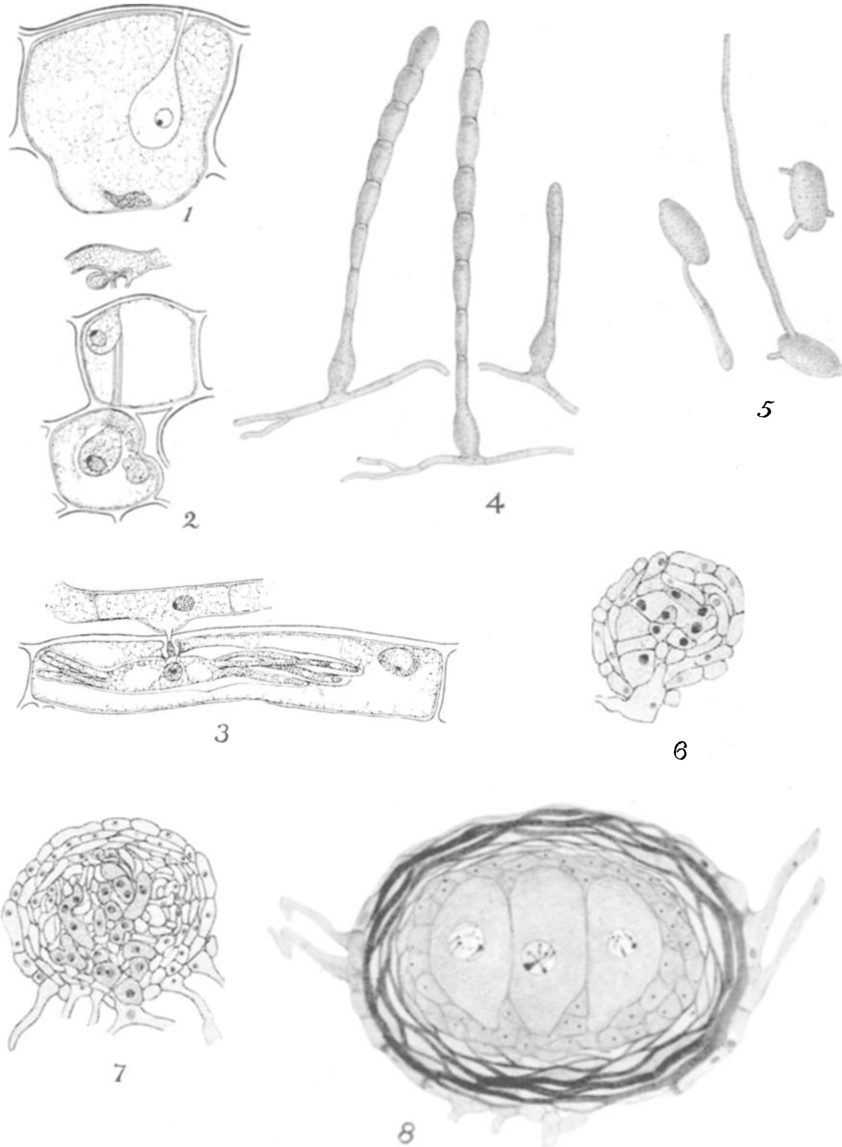

Plate XIII

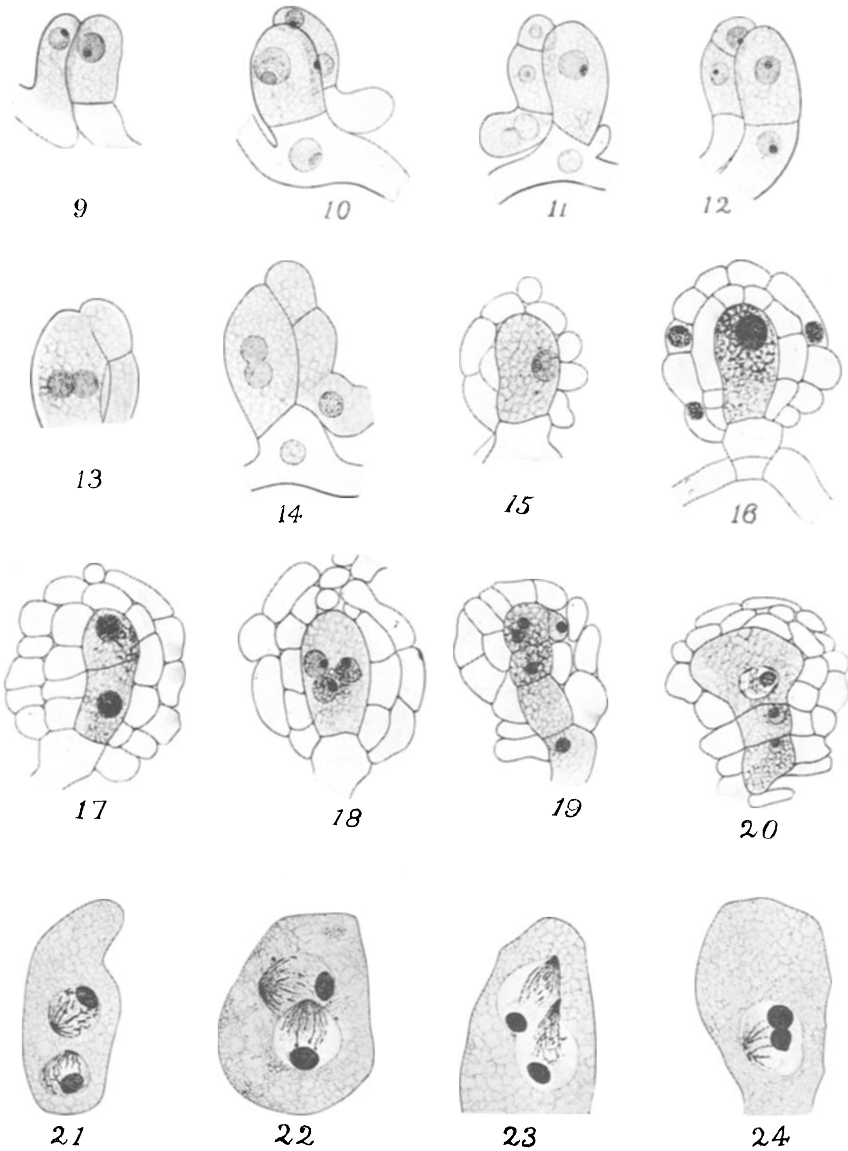

PLATE XIV

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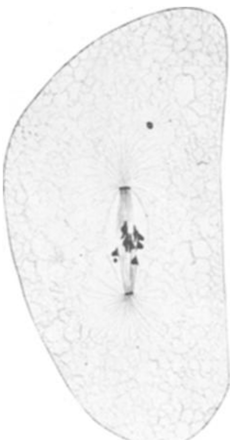

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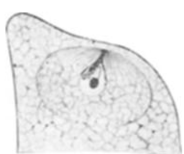

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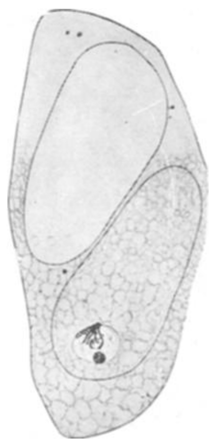

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Plate XV

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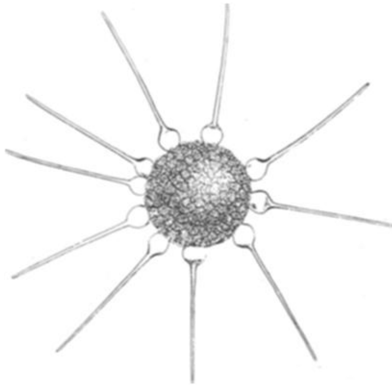

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34a

35a

36a

37

38

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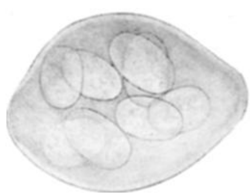
37a



38a

39a

PLATE XVI